

A MATHEMATICAL MODEL FOR CIRCUMNUTATIONS

Helge Andersen

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ABSTRACT

A mathematical model describing a circuit of a transformer with a magnetic core is presented. The model is based on the assumption that the magnetic field is uniform in the core and that the magnetic flux is constant in the core. The model is used to study the effect of the magnetic field on the transformer's performance.

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The second part of the paper contains a detailed description of the mathematical model of the previously published model for only plane magnetization.

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ABSTRACT

A mathematical model describing circular or elliptical plant movements around the plumb-line has been developed. Such growth movements, usually termed circumnutations, are explained as delayed geotropic reactions of the plant due to gravitational stimulations received during these movements.

The present model is an extension of a previously published model treating only the case of oscillatory movements in a plane, where the plant rhythmically passes the plumb-line.

The model is non-linear, and as a new feature it includes the possibility of taking asymmetric plants into consideration.

In the first part of the paper it is shown that these features implicate non-trivial theoretical predictions concerning period, amplitude and direction of rotation of the circumnutations. Theoretical results, under different conditions, are derived and experimentally tested. Clinostat treatment of the plants is simulated. Finally theoretical and experimental results are compared with earlier reports in the literature.

The second part of the paper contains a detailed description of the mathematical extension of the previously published model for only plane oscillations.

INTRODUCTION

The present paper contains a study of so-called circumnutations in sunflower hypocotyls, i.e. of helical movements in space performed by the plants during growth. Studies of such movements in sunflower have been published by Darwin (1880) and Gradmann (1927). Israelsson and Johnsson (1967) proposed a mathematical model of the movements. The model describes circumnutations of sunflower seedlings as a geotropic phenomenon and exploits the fact that there is a considerable time delay between a gravitational stimulation and the following geotropic reaction. The model can predict certain features of the movements of the hypocotyls and a series of experimental tests have not disproved the basic tenets of the theory (Johnsson and Israelsson 1968, 1969, Andersen and Johnsson 1972, Johnsson 1974).

However, as published the model has one obvious weakness. It considers movements in one plane only, the movements being described by the bending of the plant with respect to the plumb-line, while circumnutations are performed in space. In earlier papers it was claimed that one could think of circular movements in space as composed of two perpendicular bendings.

This is not possible, unless in the limiting case of very small bending angles, merely because of the reason that turnings around perpendicular axes are non-commutating. Furthermore, even if this difficulty could be overcome, the description of circular movements as composed of two perpendicular bendings is unsatisfactory for at least 3 reasons.

1. The system describing the plant must be non-linear and thus two motions cannot be added in a simple way (the so-called superposition principle is not valid).
2. It is not possible to take asymmetries of the plants into consideration. Asymmetries are natural to introduce, since the direction of rotation is not evenly distributed in a population of sunflower hypocotyls. Most of the plants rotate in counterclockwise direction (when seen from above).
3. It is difficult to simulate the action of clinostat rotation on the plants.

An extension of the mathematical model in order to describe circum - nutations in space, which is the natural behaviour of the plants, was therefore desirable.

The present paper, in which this extension is made, consists of two parts, I and II. Part I contains a qualitative treatment of the three points mentioned above, followed by quantitative theoretical and experimental results. Part II describes in detail the mathematical extension of the model. The extension is of general nature, but will be used only to derive quantitative theoretical results in the three cases above.

Background knowledge of the cited papers is of value when reading the present paper. Differential equation, values of constants etc. in the text refer, if not otherwise stated, to the version of the model for bendings in a plane as used in Andersen and Johnsson 1972.

Part I

QUALITATIVE DISCUSSION

1. The necessity of non-linearities.

The starting point for the mathematical description of the bendings in a plane, plane oscillations, of the sunflower hypocotyl was the following equation

$$\frac{d\alpha}{dt}(t) = -k \cdot \alpha(t-t_0) \quad (\text{Israelsson and Johnsson 1967})$$

where α is the deflection angle of the hypocotyl with respect to the plumb-line, t_0 the time delay mentioned in the introduction and k a positive constant. The minus sign in the right member of the equation indicates that the reaction, represented by $\frac{d\alpha}{dt}$, is directed contrary to the deflection of the plant t_0 minutes earlier.

This difference - differential equation has oscillatory solutions for certain values of k and t_0 . However, for any value of t_0 , the amplitude of the oscillations is stable only for one discrete value of the constant k (depending on t_0). The equation is therefore not physiologically realistic.

A more realistic equation is.

$$\frac{d\alpha}{dt}(t) = -k \cdot \sin \alpha(t-t_0).$$

The sine-function was introduced into the right member of the equation because this member represents the geotropic stimulation of the plant which, for small angles, is thought to be proportional to the component of gravity at right angles to the plant.

If the constant k is suitably chosen, this equation gives stable oscillations, due to the non-linearity in the sine-function.

In circular circumnutations the angle α is constant, see Figure 1. The change of angle per unit time (corresponding to $\frac{d\alpha}{dt}$ in the model for plane oscillations) is

$$\sin \alpha \frac{d\phi}{dt} \quad \text{according to Figure 1.}$$

Hence, for circular circumnutations we get

$$\sin \alpha(t) \frac{d\phi}{dt}(t) = k \cdot \sin \alpha(t-t_0) \quad \text{or} \quad \frac{d\phi}{dt} = k$$

since α is constant.

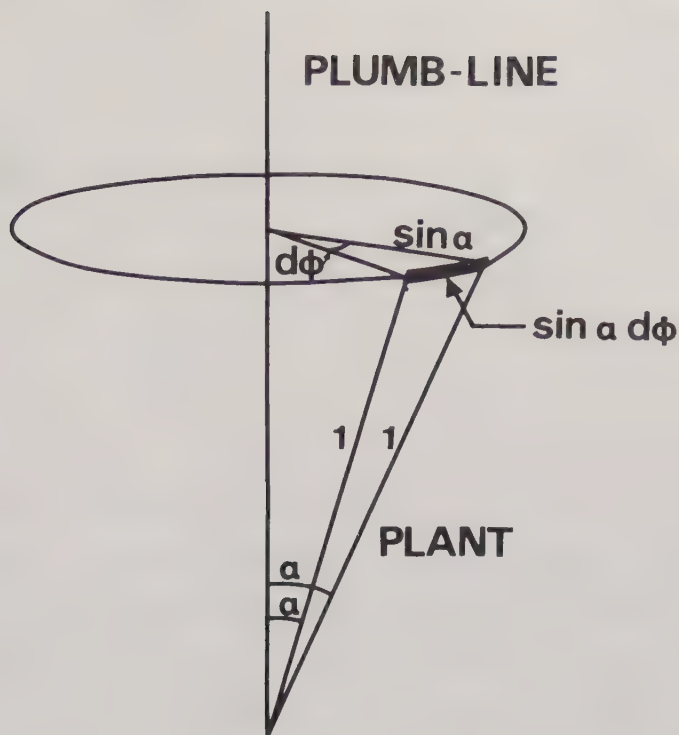


Figure 1. Circular circumnutations with amplitude α .

With an angular velocity of $\frac{d\phi}{dt}$, the angle passed through by the plant per unit time is $\sin \alpha \frac{d\phi}{dt}$ as indicated.

We have dropped the sign of k since for the moment we are only interested in the magnitude of $\frac{d\phi}{dt}$. The directional properties of the reaction will be considered in connection with Figure 2.

In this simple qualitative model the angular velocity $\frac{d\phi}{dt}$ equals $\frac{90^\circ}{t_0}$ (degrees/minute) since the plant has to turn 90 degrees during the time t_0 in order to react at the right moment, i.e. when the growth reaction has the same direction as the velocity, see Figure 2A.

The equation above is independent of α , i.e. the circumnutation can have any amplitude and is consequently unstable.

In order to achieve stable circumnutations some kind of non-linearity has to be introduced. Such a non-linearity (logarithmic) was introduced by Johnsson (1971) on purely physiological grounds, and has been used in Andersen and Johnsson 1972.

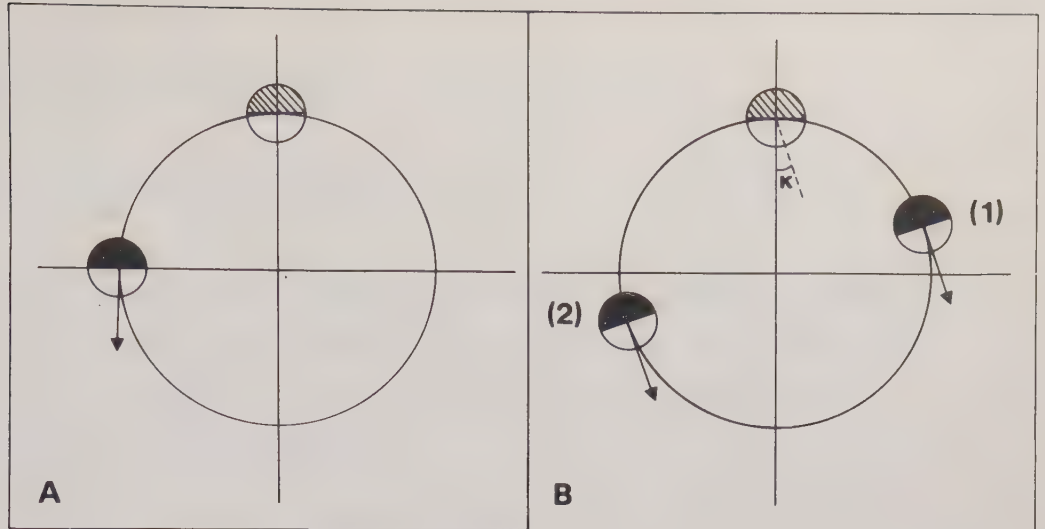


Figure 2. Circular circumnutations, seen from above.

The small circles represent sections through the plant stem which moves along the circular path during the circum - nutation. The base of the plant stem can be thought of as situated in the middle of the path. The plant receives a gravitational stimulation at the top of its circular path and the hatched area will get a higher growth hormone concentration. After the time t_0 the shaded side will grow faster than the opposite one causing a growth reaction in the direction of the arrow. In order to sustain the circumnutation the reaction must always have the same direction as the velocity.

2A: For a symmetrical plant this will occur when the plant travels 90 degrees in either direction during the time t_0 . Since the two cases thus obtained are equivalent only one is indicated in the figure.

2B: For an asymmetrical plant (asymmetry κ) it will occur when the plant travels $(90^\circ - \kappa)$ in clockwise direction or $(90^\circ + \kappa)$ in counterclockwise direction. These cases are not equivalent and are both shown in the figure.

With this logarithmic non-linearity our equation becomes

$$\sin \alpha(t) \frac{d\phi}{dt}(t) = A \cdot \ln(1 + B \cdot \sin \alpha(t - t_0))$$

or

$$\frac{d\phi}{dt} = \frac{A}{\sin \alpha} \cdot \ln(1 + B \cdot \sin \alpha)$$

since α is constant in circular circumnutations.

A and B are constants replacing the constant k above.

With $\frac{d\phi}{dt} = \frac{90^\circ}{t_0}$ (degrees/minute) we get

$$\frac{90^\circ}{t_0} = \frac{A}{\sin\alpha} \cdot \ln(1 + B \cdot \sin\alpha). \quad 0^\circ < \alpha \leq 90^\circ$$

In this equation the right member is a strictly decreasing function of α and thus there is at most one value of α that can satisfy the equation. This value, if it exists, will be the steady state amplitude of the circumnutations.

2. Asymmetry.

Up till now we have assumed that a plant always reacts geotropically in a direction opposite (180°) to the geotropic stimulation. We now introduce an asymmetry κ in the plant. The asymmetry means, that instead of reacting in the direction 180° relative to the stimulation, the plant reacts in the direction $180^\circ + \kappa$ relative to the stimulation. κ can be positive or negative, but we shall presume κ to be positive without loosing generality.

Due to the asymmetry the situation illustrated in Figure 2A has to be somewhat modified. The velocity of the plant is tangent to the circle in which the plant rotates. Hence the plant must be in one of the two positions where the tangent of the circle is parallel to the direction in which the plant reacts to a stimulation t_0 (minutes) earlier.

This is principally the same reaction condition for sustained circum - nutation that was discussed above for the situation in Figure 2A.

Also in that situation one might think of two cases. They are, however, equivalent and only one is shown in Figure 2A. With asymmetry, on the contrary, the two cases are not equivalent and therefore both of them, (1) and (2), are shown in Figure 2B.

Mathematically this means that for circular movements of the plant the condition $\frac{d\phi}{dt} = \frac{90^\circ}{t_0}$ has to be replaced by

$$(1) \quad \frac{d\phi}{dt} = \frac{90^\circ - \kappa}{t_0} \quad \text{or} \quad (2) \quad \frac{d\phi}{dt} = \frac{90^\circ + \kappa}{t_0}$$

For circular circumnutations we had

$$\frac{d\phi}{dt} = \frac{A}{\sin\alpha} \cdot \ln(1 + B \cdot \sin\alpha).$$

Put together these conditions give the following two equations

$$(1) \quad 90^\circ - \kappa = t_0 \frac{A}{\sin \alpha} \cdot \ln(1 + B \cdot \sin \alpha) \quad 0^\circ < \alpha \leq 90^\circ$$

$$(2) \quad 90^\circ + \kappa = t_0 \frac{A}{\sin \alpha} \cdot \ln(1 + B \cdot \sin \alpha) \quad 0^\circ < \alpha \leq 90^\circ$$

Since the right members are strictly decreasing functions of α with maximum value $t_0 AB$ ($\alpha \rightarrow 0^\circ$) and minimum value $t_0 A \cdot \ln(1 + B)$ ($\alpha = 90^\circ$) principally the following four cases can occur.

- a. None of the left members of the equations (1) and (2) lies between the maximum and the minimum. There is no value of α that satisfies any of the equations. The plant cannot perform stable circumnutations.
- b. The left member of eq. (1) lies between the maximum and the minimum while the left member of eq. (2) is too large. Only eq. (1) has got a solution. This means that the plant can only rotate clockwise (seen from above), see Figure 2B. The period is longer than for the corresponding symmetrical plant (period $T_1 = \frac{360t_0}{90 - \kappa}$ instead of $T = \frac{360t_0}{90} = 4t_0$), since the plant moves less than 90° during the time t_0 .
- c. The left member of eq. (2) lies between the maximum and the minimum while the left member of eq. (1) is too small. Only eq. (2) has got a solution. This means that the plant can only rotate counter-clockwise, see Figure 2B. The period is shorter than for the corresponding symmetrical plant (period $T_2 = \frac{360t_0}{90 + \kappa}$ instead of $T = \frac{360t_0}{90} = 4t_0$), since the plant moves more than 90° during the time t_0 .
- d. The left members of both equations lie between the maximum and the minimum. The plant can rotate clockwise as well as counterclockwise. The circumnutations in the two different directions will have different periods T_1 and T_2 resp. and also different amplitudes.

Which one of the four cases that will actually occur depends on the values of A , B and κ . Suppose that A and B are chosen to give circumnutations with an amplitude α about 20° for a symmetric plant (compare results below). This means that both equations have got the solution $\alpha \approx 20^\circ$ for $\kappa = 0^\circ$. It is evident that for a very small value of the asymmetry κ both eq. (1) and (2) can still be solved, that is case d. above is valid.

An increase of the asymmetry will implicate that only one of the equations can be solved, case b. or c., and further increase of κ should give case a.

An increase of the degree of non-linearity, represented by the constant B , with the same amplitude α for $\kappa = 0^\circ$ means decrease of A and it also means that there is a larger difference between the maximum value t_0AB and the minimum value $t_0A \cdot \ln(1 + B)$ above.

Consequently the intervals, in which κ may be chosen in order to get the cases d. and b. or c. are broadened.

These qualitative results, especially the possibility of having a plant rotating clockwise as well as counterclockwise, will be tested quantitatively both theoretically and experimentally.

3. Clinostat treatment.

So-called clinostat treatment consists of a slow rotation of the plant around an axis, oblique to the plumb-line. A typical value of the rotation speed is 1 rpm, but both higher and lower speeds have been reported. The geotropically sensitive organs of the plant are usually mounted parallel to the rotation axis. The clinostat with horizontal axis has a principally very important application in the studies of geotropic phenomena, since the gravitational force will then stimulate the plant uniformly around its rotating stem. The preference of the plumb-line direction is thereby excluded, which is thought to simulate zero-g conditions. In the present paper we will only discuss results from clinostats with horizontal axes.

In the model for plane oscillations, clinostat treatment can only be simulated by giving the plant repeated alternating gravitational pulses on each side (Johnsson 1974). In the extended model the stimulations can be distributed around the stem as in reality. Specifically the simulation includes a certain direction of the clinostat rotation of the plant. This could of course not be achieved in the previous model.

RESULTS

Theoretical as well as experimental results will be given. Concerning the theoretical results it has already been mentioned that we, if not otherwise stated, have used the same values of constants as in Andersen and Johnsson 1972. Concerning the experimental results it should be emphasized that only predictions from the model leading to previously unknown results have been tested. Well established experimental facts, such as the existence of circumnutations in sunflower hypocotyls, or that these cease on the clinostat have been verified earlier. In the experiments we used the same experimental material and cultivating method as in Andersen and Johnsson 1972.

1. Circumnutations in the extended model.

A symmetrical theoretical plant cannot by itself start circumnutations, even if it is already performing plane oscillations. In order to start circumnutations in a symmetrical plant it has to be stimulated in two different directions at different times. This is not necessary for real plants, even if they are symmetrical. They can start elliptical circumnutations because of small spontaneous movements in all directions, not included in our model. The passage from plane to elliptical and ultimately circular oscillations occurs succesively in most cases and can be rather slow.

Figure 3 shows the path, calculated from the equations in part II, of a symmetrical plant which was first stimulated in the y-direction and 40 minutes later in the x-direction. The figure shows, like the following figures of the same type, the projection from above of the top of the plant onto a horizontal plane, the x-y-plane.

After a few revolutions the plant reaches steady state with the period $T = 155$ min and the amplitude $\alpha = 20.3^\circ$. These values are to be compared with the period 157 min and the amplitude 24.2° for the corresponding plane oscillations. The latter values should have been valid also for circumnutations considered as composed of two perpendicular plane oscillations. The differences are due to the non-linearity in the model and confirm what we have already stated. Two non-linear oscillations cannot be composed to circular circumnutations in the simple way applicable to linear oscillations.

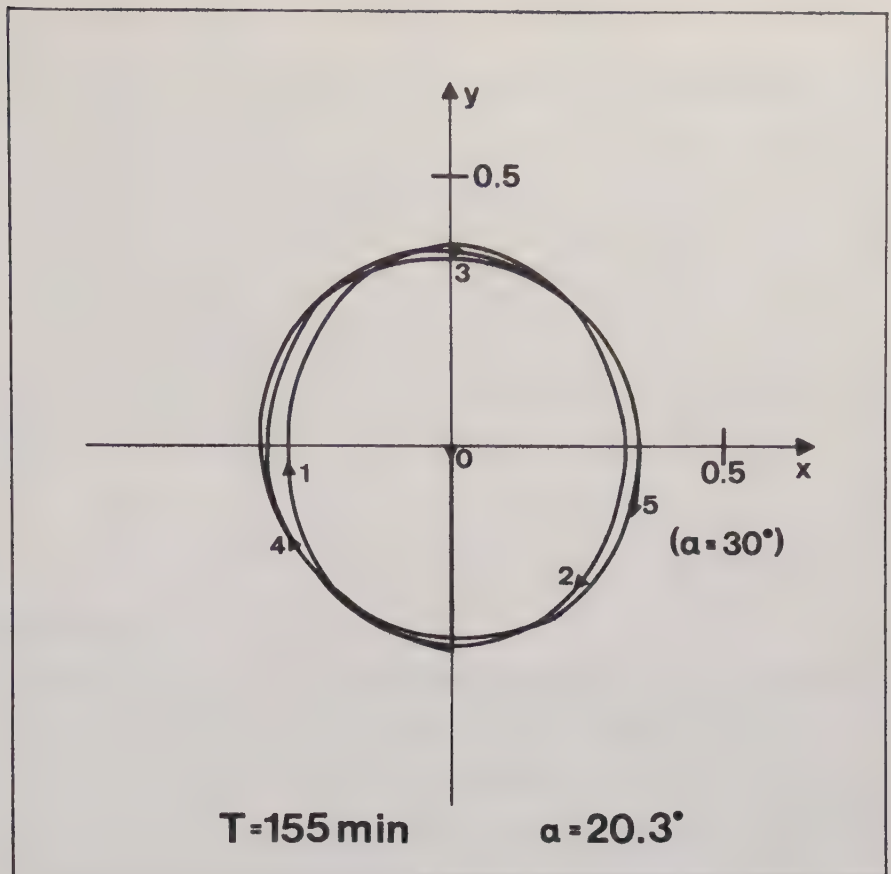


Figure 3. Circumnutations of a symmetrical plant.

The figure shows the top of a theoretical plant of unit length projected from above onto the x-y-plane. The circumnutations were started by two subsequent 10 minute pulses applied with 40 minutes time-lag. The steady state period T and amplitude α are indicated in the figure. Values of the time t (in units of hundred minutes), counted from the beginning of the first starting pulse, are also included.

With different response magnitudes in the x- and y-directions, it is possible to achieve elliptical circumnutations. The eccentricity of such an ellipse depends on the quotient between the two response magnitudes. As far as we have been able to check, all the results for circular circumnutations given in the present paper, are principally valid also for elliptical circumnutations. We will therefore, when presenting the results, restrict our attention to circular circumnutations.

For a symmetrical plant, the direction of rotation is determined exclusively by the starting pulses. If the 'x-pulse' above had been applied in the negative x-direction the plant would have rotated in the opposite direction. It should be observed that this is valid also for elliptical circumnutations, in which the plants are not axially symmetric, but still reflection symmetric.

The asymmetry of the present paper is of the latter kind and we are now going to study the implications of it.

2. Asymmetry.

Theoretical results.

Contrary to a symmetrical plant, the circumnutations of an asymmetrical plant can be started by only one starting pulse. This is shown in Figure 4A, where $\kappa = 9.0^\circ$ and all other parameters unchanged. From the figure it is evident that the asymmetrical plant, seen from above, always reacts to the left (positive κ) with respect to the direction in which a symmetrical plant would have reacted. Thus the movements of an asymmetrical plant will deviate more and more from plane oscillations and finally become circular. Because of the left-reactions, the direction of rotation will be clockwise, the natural direction of rotation with positive κ . We have got case b. or d. in the qualitative discussion and, as expected, the period $T = 166$ min and the amplitude $\alpha = 31.2^\circ$ are larger than for a corresponding symmetrical plant.

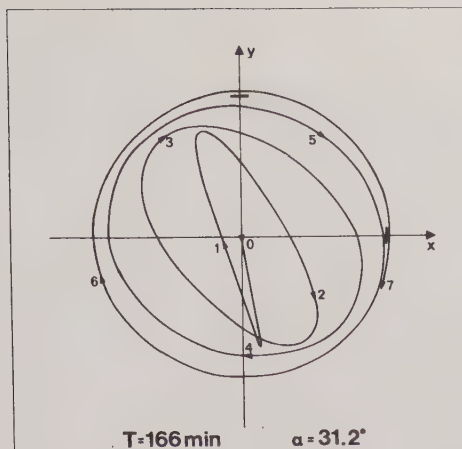
However, the period $T = 166$ min is not exactly equal to the period $T_1 = \frac{90}{90-9} \cdot 155 \text{ min} \approx 172 \text{ min}$ in the qualitative discussion. This is so because the model used in the simulations is considerably more complex than the discussion model.

The plant can also be started by two pulses, like the symmetrical plant in Figure 3. Figure 5A shows the result when the asymmetrical plant was first stimulated in the y-direction and 40 minutes later in the x-direction, i.e. exactly the same combination of starting pulses as in Figure 3. The plant rotates in clockwise direction, with the same period and amplitude as in Figure 4A. If the x-stimulation is instead applied in negative x-direction it might be possible to achieve counterclockwise circumnutations as well (case d.). The result is shown in Figure 6A. The plant rotates a few revolutions in counterclockwise direction, but the spirals degenerate more and more until they change into plane

A

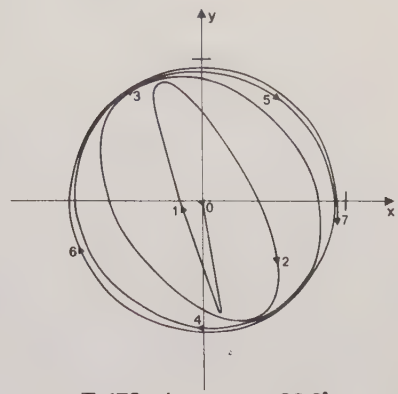
B

4.

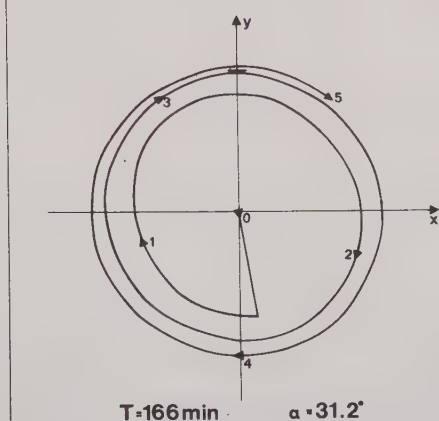


$T=170\text{min}$

$\alpha=28.0^\circ$

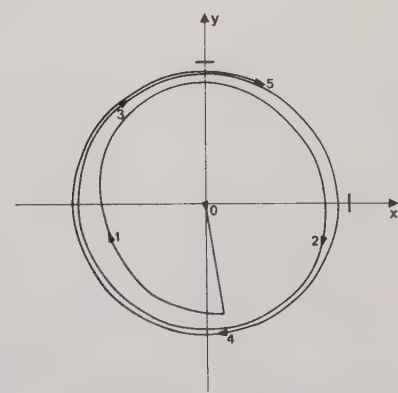


5.

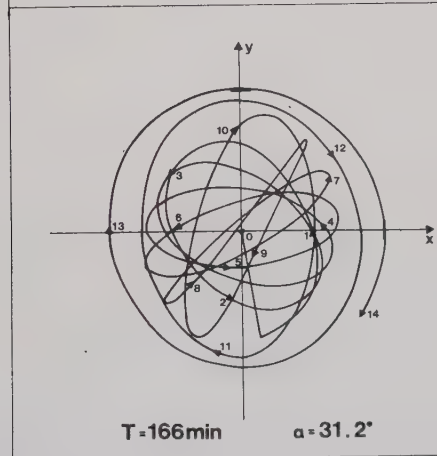


$T=170\text{min}$

$\alpha=28.0^\circ$



6.



$T=146\text{min}$

$\alpha=17.8^\circ$

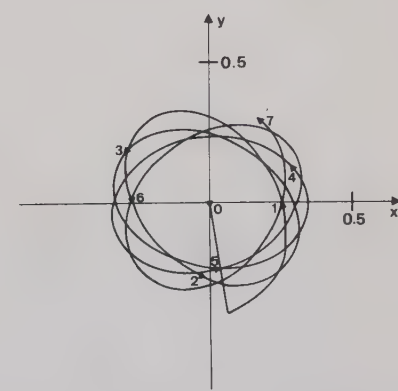


Figure 4-6. Circumnutations of asymmetric plants, with asymmetry $\kappa = 9.0^\circ$. The non-linearity of the plants in column B is 4 times larger than of those in column A. For other details see Figure 3.

- 4: Started with one pulse, the plants are rotating in their natural direction of rotation, i.e. clockwise when κ is positive.
- 5: Started in the natural direction of rotation by two pulses at different times, the plants continue in this direction.
- 6: The plants are started contrary to the natural direction of rotation by two pulses. In Figure 6A the plant rotates a few revolutions counterclockwise, but finally turns back to its natural clockwise rotation. With larger non-linearity as in Figure 6B, stable counterclockwise circumnutations can be achieved.

oscillation and ultimately into clockwise circumnutation.

We cannot exclude the possibility that some other combination of starting pulses (stronger, weaker, longer or shorter time between the pulses) might give a final counterclockwise rotation, but about 30 different combinations have been tried without success. Either is the asymmetry too large or the degree of non-linearity too small for the plant to be able to rotate in counterclockwise as well as in clockwise direction. We have got case b. in the qualitative discussion.

In order to test if it was possible to achieve case d. we decided to increase the degree of non-linearity. Alternatively, the asymmetry could have been decreased.

The values of A and B hitherto used, i.e. the values from Andersen and Johnsson 1972, will be called the normal values of A and B.

The normal value of B was multiplied by 4 and the normal value of A adapted so as to give normal period $T = 155$ min and amplitude $\alpha = 20.3^\circ$ for a symmetrical plant. Then the same three pulse combinations as before were applied to the corresponding asymmetrical plants, with asymmetry $\kappa = 9.0^\circ$. The results are shown in Figure 4B, 5B and 6B respectively. For the clockwise rotation in Figure 4B and 5B the period and amplitude have changed a little to 170 min and 28.0° resp., but principally the results are similar to those of Figure 4A and 5A. In Figure 6B there is a decisive difference. The plant can in fact rotate in counterclockwise direction. The steady state, which is reached only after many revolutions, has the period 146 min and the amplitude 17.8° , i.e. less than for the corresponding symmetrical plant, as expected. We have got case d. in the qualitative discussion.

It should be observed that, although both directions of rotation are possible, the present plant chooses clockwise direction when no direction of rotation is forced upon it (Figure 4B). Hence, in case b. and d., the natural direction of rotation is clockwise.

Now only case c. is missing. A somewhat extended qualitative discussion clarifies that a large degree of non-linearity and a large asymmetry should be in favour of this case. As a matter of fact the extended discussion indicates that the case should be present as soon as the degree of non-linearity exceeds its normal value. However, we have not been able to find this case, although we have used values of B up to 1000 times larger than normal and tried a lot of different starting-pulse combinations.

We have even tried a better mathematical approximation in the model but in vain. At the present stage, we have no explanation for the absence of case c. in the simulations and can only state, by experience, that the oscillations always degenerate when case c. is attempted.

We have already seen that $\kappa = 9.0^\circ$ gave case b. with the normal value of B. If this value was multiplied by 4 we got case d. Also with this larger value of B it is possible to choose κ so large that the plant can only rotate in clockwise direction, i.e. case b. It turns out that the boundary between the two cases d. and b. is now given by $\kappa = 9.5^\circ$. If κ is further increased we will get case a. The boundary between b. and a. is given by $\kappa = 37.5^\circ$.

Corresponding boundary values of κ were calculated for other values of B, being 1/8, 1/4, 1/2, 1, 2, 4 and 8 times the normal B-value. In Figure 7 the boundary values of κ are plotted against these factors in order to show where transitions occur between the cases d., b. and a. The figure confirms our qualitative argument. The larger degree of non-linearity, the larger asymmetry can be tolerated in the cases d. and b. The figure includes values of κ around 40° , but such values must be judged as quite unrealistic for sunflower and have been included only to map the passage between the different cases.

It might be possible to determine κ experimentally, but this is not done in the present paper. The degree of non-linearity cannot be easily determined from experiment. Our normal value has been indirectly determined on relatively vague foundations (Johnsson 1971). However, it gave reasonably good agreement with experiments in Andersen and Johnsson 1972 and by varying the non-linearity factor from 1/8 to 8, it is likely that the actual values are included among those of Figure 7.

The theoretical results can then be summarized.

The plant has a natural direction of rotation dependent upon the sign of the asymmetry κ .

The presence of a characteristic direction of rotation is known. The present contribution is based on the idea that this direction of rotation is due to internal features and not to external influences (Corioli forces and the like, cf. Israelsson and Johnsson 1967).

If, and only if, there is a suitable relation between the magnitude of asymmetry and the degree of non-linearity, corresponding to the area d. in Figure 7, the plant can perform stable circumnutations contrary to the natural direction of rotation. In doing so its period and also its amplitude will be smaller than in the natural direction of rotation. This means that by suitably applied gravitational pulses, at least some plants might be brought to rotate contrary to their natural direction of rotation. Period and amplitude should then change as mentioned. For the rest of the plants this is not possible. These conclusions can be tested experimentally and that will be the topic of the next section.

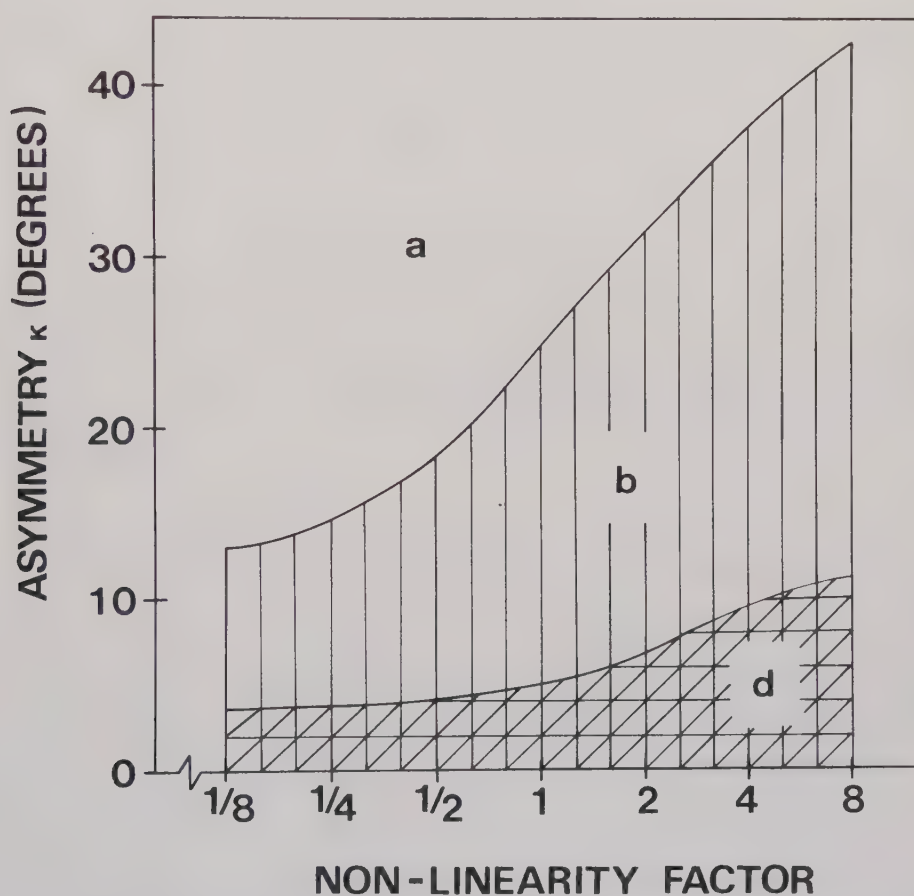


Figure 7. Asymmetry κ as a function of the degree of non-linearity. The ordinate 1 corresponds to the normal B-value.

- Area a: Circumnutations are not possible.
- Area b: Circumnutations can be performed only in the natural direction of rotation, i.e. clockwise with positive κ .
- Area c: Circumnutations should be performed only in counter-clockwise direction (this case was never found in the quantitative calculations and is therefore not included).
- Area d: Circumnutations can be performed in clockwise as well as counterclockwise direction.

Experimental results.

The sunflower hypocotyls were allowed to grow undisturbed until they had reached a length of 30-40 mm and begun to perform circumnutations. We presume that the plants were all rotating in their natural direction of rotation.

Then the horizontal projection of the direction in space of the hypocotyl was noted down every 30 minutes for 10 hours. In this way we could determine the direction of rotation and get a fairly good estimate of the period. The amplitude was not determined.

When the direction of rotation had been determined, a gravitational pulse (60° tilting during 20 minutes) was applied at right angles to every hypocotyl, so as to change the direction of rotation. In all but a few cases this pulse was sufficient to change the direction of rotation, at least temporarily.

After the pulse the plants were allowed to rotate freely for 24 hours. During the first 2-3 hours of this time it was checked that the plants had, temporarily, changed direction of rotation. During the last 10 hours of these 24 hours, the direction of rotation and the period were again determined.

Since the result of the first determination was immediately used, it is realized that the observations had to be visual instead of photographic as in earlier works. The projection of the direction in space of the plant can be relatively precisely determined also by direct observation without a protractor, and therefore the period can be regarded as well-determined (estimated additional error compared to photographic determinations 1 %).

As mentioned the aim of the experiments was to investigate if any plants could rotate contrary to their natural direction of rotation and, if so, to check the theoretically predicted shortening of the period.

Concerning the second test, it has to be remembered that the circumnutation periods which are to be compared, are determined with an interval of 24 hours. During this time the plants grow and their parameters change in such a way that the period is increased.

Therefore we should not expect an absolute decrease of the periods of those plants that have changed their direction of rotation. Instead we have to compare their increase of the mean period with that of a reference group. As a reference group we chose those plants that

turned back to their initial direction of rotation. This choice is not undisputable and will be discussed below.

126 plants were used in the experiments. Of these 12 had to be rejected because they did not react satisfactorily to the gravitational pulse mentioned above, stopped oscillating during the experiment or had amplitudes above 90° at the end of the experiment.

Among the rest of the plants 93 initially rotated counterclockwise and 21 rotated clockwise. Depending on direction of rotation during the last 10 hours of the experiment the plants can be divided into 4 groups, denoted Co-Co, Co-C1, C1-C1 and C1-Co, where Co stands for counterclockwise and C1 for clockwise.

For every plant the quotient between the period during the last 10 hours and the period during the first 10 hours was calculated. For every group the mean value and the standard deviation of the mean

$$\left(\sqrt{\frac{\sum_i (x_i - x_m)^2}{n(n-1)}} \right) \quad \text{were calculated for these quotients and}$$

also for the initial periods.

The result is shown in the following table.

First 10 h	Counterclockwise		Clockwise	
Number	93		21	
Period (min)	153 ± 3	168 ± 3	204 ± 18	166 ± 8
Last 10 h	Co	C1	C1	Co
Number	41 + (10)	42	3 + (4)	14
Quotient	1.56 ± 0.05	1.51 ± 0.04	1.43 ± 0.08	1.32 ± 0.05

These results for sunflower hypocotyls have not been previously reported and they are not becoming less interesting by the fact that they were first theoretically predicted and then experimentally found.

In addition to the main results above, we made some other observations worthy of being mentioned.

In the first place, the ratio between the initially clockwise and counterclockwise rotating plants is 21:93, which should be compared to 25 % : 60 % in Israelsson and Johnsson 1967. In this earlier work 15 % of the plants were oscillating in one plane. We also encountered a few such plants, but they were excluded before the start of our experiments. Considering the random choice of plants and the relatively small number of clockwise rotating plants, the agreement is acceptable.

In the second place, the period of the circumnutations in the present paper was 163 ± 22 minutes, which should be compared to 157 ± 17 minutes for the plane oscillations in Andersen and Johnsson 1972. Considering our theoretical prediction that the period should be somewhat longer for an asymmetrical plant rotating in its natural direction of rotation (theoretically from 155 min for $\kappa = 0^\circ$ to 166 min for $\kappa = 9.0^\circ$ according to Figures 3 and 4A) the agreement must be judged as good.

In the third place, there is a significant difference between the initial mean periods of the plants in the Co-Cl-group and the Co-Co-group. If this difference had been due to different asymmetry, a natural assumption since the magnitude of asymmetry influences the period and also the tendency of returning to the initial direction of rotation, the Co-Co-group would have had the longer mean period. This is not the case however, and we have no straightforward explanation of this anomaly. Some speculations will be presented in the discussion.

3. Simulations of clinostat treatments.

The extended model is well suited for simulations of clinostat experiments. The action of the clinostat with horizontal axis can be simulated by applying gravitational stimulation pulses successively around the stem of the plant, at a speed corresponding to the turning speed of the clinostat axis.

In such simulations the following details should be observed.

Up to now the angle between the axis of the plant and the plumb-line has never exceeded 90° . On the clinostat with horizontal axis this angle will sometimes exceed 90° . The model allows this, but the relation between the angle and the geotropic stimulation is then probably not a sine function (cf. Andus 1964, Larsen 1969, Johnsson 1974). In this paper, however, we will restrict ourselves to the sine dependence, although more realistic and complex functions could be included in the model.

Since the gravitational pulses are applied in a discrete way, a certain attention has to be paid to the problem of distributing them uniformly around the stem of the plant. With an iteration interval of 1 minute in the calculations and a clinostat speed of 1 rpm = $360^\circ/\text{min}$ the plant would always be stimulated in the same position, which, obviously, would disagree with the experimental, omnilateral stimulation. With a clinostat speed of 5 rad/min $\approx 286^\circ/\text{min}$ the pulses will be given in the positions $\phi_0 = 0^\circ$, $\phi_1 = 286^\circ$, $\phi_2 = 573^\circ$, $\phi_3 = 859^\circ$ etc. This gives a good approximation of omnilateral stimulation. (Since the circumference of the unit circle is an irrational number, clinostat speeds in fractions of radians per minute will never give two stimulation pulses in exactly the same position).

In all the simulations the rotation of the clinostat was clockwise (seen from above) and symmetric as well as asymmetric plants ($\kappa = \pm 9.0^\circ$) were used.

The clinostat rates most often employed in experiments, i.e. ca 1, 0.5 and 0.2 rpm, provided the following results.

Clinostat action simulated without previous gravitational stimulation of the plants: The plants showed initial curvatures of $1^\circ - 3^\circ$ followed by cessation of the movements.

Clinostat action simulated after previous gravitational stimulation of the plants (30° , 60° or 90° tilting during 10 minutes): The plants reacted geotropically to the stimulation and reached a certain angle determined by the gravitational pulse. They stopped at this angle for the rest of the simulations.

Clinostat action simulated after previous normal circumnutations of the plants: The movements of the plants ceased 30-40 minutes after the start of the clinostat treatment. The positions of the plants were then fixed during the rest of the simulations.

These results are valid for the mentioned clinostat rates and for symmetric as well as asymmetric plants (independent of the sign of κ). They are in agreement with the experimental results on sunflower (cf. Johnsson 1974).

If the clinostat rate was lowered to 0.1 - 0.04 rpm, i.e. 1 revolution in 10 - 25 minutes, the plants performed irregular movements with a magnitude of 5° - 10° . There was still no noticeable difference between symmetric and asymmetric plants.

If the clinostat rate was further slowed down, 1 revolution in 50 - 100 minutes, the plants performed entrained circumnutations with minor differences in amplitude and range of entrainment between the three types of plants ($\kappa = 0^{\circ}$, $\pm 9.0^{\circ}$).

DISCUSSION

The present paper is mainly of theoretical nature. A quantitative mathematical model for the circumnutations of sunflower is developed and the behaviour of this model investigated. For the corresponding experimental studies and previous theoretical ideas we have already referred to the papers by Israelsson and Johnsson 1967, Johnsson and Israelsson 1968, 1969 and Johnsson 1971, 1974 which form the foundation of the present mathematical model. We also wish to emphasize the early experimental works of Gradmann 1921, 1927. Experimental studies of circumnutations in Sicyos angulatus, rather closely related to the theoretical studies of the present paper, were performed by Gradmann 1921. Although he used another material, there are striking similarities between his results and those of the present paper. Compare for instance his figures of experimental circumnutations to our Figures 3 - 6.

There are also results that we do not recognize which is natural since he did not use sunflower, but at least some of these results might be due to the varying temperature- and light-conditions of his experiments. In principle Gradmann applied the same theoretical model for circumnutations that is used in this paper (a delayed geotropical overcompensation) but he never made a complete mathematical formulation of his ideas, which makes some arguments difficult to understand.

In Gradmann's material there was no preferred direction of rotation, and it was also possible for all plants to rotate in clockwise as well as in counterclockwise direction. Thus he had of course no reason to consider asymmetrical plants and, assuming neglectable asymmetry, his results are consistent with our theory.

We have assumed that the preferred direction of rotation in sunflower is due to some internal asymmetry. The experiments of the present paper, which our theoretical results encouraged us to perform, support this idea. For, assuming a direction of rotation due to external influence, it would be difficult to explain why some plants return to their initial direction of rotation while others don't. However, the evidence is still indirect and more direct observations of the asymmetry are desirable. This might, for instance, be done by careful observations of plants reacting to gravitational pulses, or still better if it is possible to find some geometrical or hormonal transport

property of the plants that can account for the asymmetry. This is not only of general interest but could also have been of value in the present work, as is shown below.

Asymmetric reactions to gravitational pulses, so-called lateral geotropic reactions, have been reported for other materials. Very big lateral geotropic reactions of Pharbitis hispida are exemplified in Rawitscher 1932.

As was pointed out above (page 20), there is a significant difference between the initial mean periods of the Co-Cl-group and the Co-Co-group that is not quite in accordance with the theory. A few possible explanations for this discrepancy will be suggested.

The theory might be wrong or incomplete.

Perhaps we have encountered the case c. that was never found in the quantitative calculations. As will be remembered, the period in this case was shorter than for the corresponding symmetrical plant, which is actually valid for the Co-Co-group.

The difference may finally be an indication that our choice of reference group is not appropriate. We know that the period increases with increasing age and development of the plants. The longer mean period of the contrary-rotating group might thus mean that the plants of that group are, on the average, more developed. If this is true, it is not appropriate to use quotients, as we have done, for the comparison between the two groups (since it is not granted that the quotient of a group is constant, independent of the development of the plants in the group). Not even a randomly chosen reference group would then do, because the plants of the contrary-rotating group would be more developed. Only plants capable of rotating contrary to their natural direction of rotation would form a satisfactory reference group. However, because of the aging of the plants the experimental time is not long enough, first to ensure this capability of the plants and then to use them as a reference group. Therefore some direct method of determining the asymmetry would have been of value in the present work.

While our experiments have not disproved the ideas in this paper, many questions remain unsettled and new experimental methods and further test experiments are desirable.

Part II.

EXTENSION OF THE MODEL

In this part of the report a detailed description of the mathematical extension, of the previous model for only plane oscillations, will be given. All quantitative theoretical results of part I were obtained from the extended model derived in this part.

All coordinate systems below are three-dimensional and orthonormalized. When a certain coordinate system occurs for the first time, it is given a name and the coordinate axes are indicated within parenthesis. A vector (indicated by a bar) will be represented by rectangular coordinates, unless otherwise stated. t denotes time.

The plant is regarded as a thin cylinder, the axis of which is the vector $\bar{r}(t) = (x(t), y(t), z(t))$ in the coordinate system S_2 (x-y-z), see Figure 8 (page 28). It is also possible to use spherical coordinates $\bar{r}(t) = (r(t), \alpha(t), \phi(t))$ as indicated in the figure. Until further notice S_2 will be fixed in space. Later, when S_2 is allowed to move, we shall keep a system S_1 fixed in space.

In the present model we do not consider the lengthening of the plant during growth and therefore the length of the plant is constant and chosen equal to unity. Hence we have only two independent coordinates and the spherical representation might seem advantageous, the more so as the angle α has the same meaning as in previous publications (Andersen and Johnsson 1972). However, for reasons stated later, we shall prefer the rectangular representation, with the possibility of calculating the angles α and ϕ .

Since the plant has got an internal structure which, among other things, remembers gravitational stimulations, we need a coordinate system S_3 (u-v-w) fixed in the plant. S_3 coincides with S_2 when the plant is standing vertically. Otherwise the w-axis coincides with $\bar{r}$. In Figure 8 the origin of S_3 has been placed at the top of the plant for illustrative purposes.

In previous papers the plant was represented to an observer by the bending angle α . The angle α satisfied a certain difference - differential equation, that described the bending of the plant in a plane.

In the present paper the plant is represented to an observer in system S2 by the vector $\vec{r}$.

Our purpose is now to find a corresponding set of difference - differential equations for the vector $\vec{r}$, to describe the movements of the plant in the observer's system S2.

It is simpler to derive these equations in S3 and then transform them to S2. Therefore the following sections will deal with

1. The relation between coordinates in S3 and S2.
2. The coordinate representation of the set of equations in system S3.
3. The transformation of this coordinate representation, according to section 1, to a coordinate representation of the set of equations in system S2.
4. Numerical methods for the solution of the equations thus obtained.
5. The application of gravitational stimulation pulses.
6. Theoretical test of the extended model in the special case of plane oscillations, earlier investigated.

1. Coordinate transformation between S3 and S2.

In order to find the relation, represented by the transformation matrix M, between the coordinates of any vector in the respective systems, we shall use the experimental result that the circumnutations are performed without torsion of the plant (see Figure 4 in Israelsson and Johnsson 1967). We may thus think of the plant reaching a certain position by direct turning from vertical position around an axis in the x-y-plane. This axis is shown as the broken line in Figure 8.

- (I) It is realized that a vector along this axis, for instance $(-\sin\phi, \cos\phi, 0)$ in system S3, has got the same coordinates in S3 and S2. Another two, linearly independent, vectors are needed to calculate the matrix M, that transforms coordinates in S3 into coordinates in S2.
- (II) The vector with the coordinates $(\cos\phi, \sin\phi, 0)$ in S3 has got the coordinates $(\cos\alpha\cos\phi, \cos\alpha\sin\phi, -\sin\alpha)$ in S2.
- (III) The vector with the coordinates $(0, 0, 1)$ in S3 has got the coordinates $(\sin\alpha\cos\phi, \sin\alpha\sin\phi, \cos\alpha)$ in S2.

The derivation of (II) and (III) is facilitated by Figure 8.

Mathematically these conditions mean

$$(I) \quad M \cdot \begin{pmatrix} -\sin\phi \\ \cos\phi \\ 0 \end{pmatrix} = \begin{pmatrix} -\sin\phi \\ \cos\phi \\ 0 \end{pmatrix}$$

$$(II) \quad M \cdot \begin{pmatrix} \cos\phi \\ \sin\phi \\ 0 \end{pmatrix} = \begin{pmatrix} \cos\alpha\cos\phi \\ \cos\alpha\sin\phi \\ -\sin\alpha \end{pmatrix}$$

$$(III) \quad M \cdot \begin{pmatrix} 0 \\ 0 \\ 1 \end{pmatrix} = \begin{pmatrix} \sin\alpha\cos\phi \\ \sin\alpha\sin\phi \\ \cos\alpha \end{pmatrix}$$

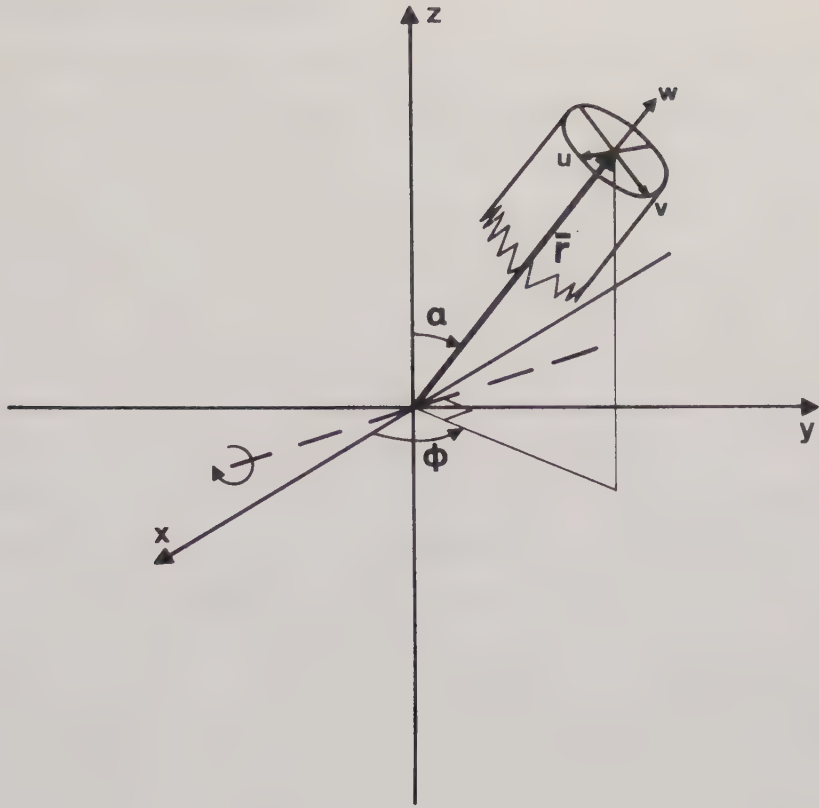


Figure 8. Coordinate system S2 (x-y-z) with the sunflower hypocotyl represented by the vector $\bar{r}$. From vertical position, the actual position of the plant is reached by turning around an axis in the x-y-plane, the axis being indicated by the broken line. The angles α and ϕ indicate magnitude and direction respectively of the turning. The coordinate system fixed in the plant, S3 (u-v-w), is shown at the top of the hypocotyl.

and from these equations

$$M = \begin{pmatrix} \sin^2\phi + \cos\alpha\cos^2\phi & \cos\phi\sin\phi(\cos\alpha-1) & \sin\alpha\cos\phi \\ \cos\phi\sin\phi(\cos\alpha-1) & \cos^2\phi + \cos\alpha\sin^2\phi & \sin\alpha\sin\phi \\ -\sin\alpha\cos\phi & -\sin\alpha\sin\phi & \cos\alpha \end{pmatrix}$$

This matrix represents a special case of rigid body rotation through Euler's angles, see Jeffreys 1946.

M^{-1} is easily calculated by exchanging ϕ for $\phi + 180^\circ$.

2. Set of equations in system S3.

In previous papers treating plane oscillations a short gravitational stimulation caused an auxin concentration deviation proportional to the measure of the stimulation. The auxin concentration deviation should not be mixed up with the auxin gradient. By the concentration deviation we simply mean the difference between the actual auxin concentration in a point of the cross section of the stem of the plant and the mean auxin concentration of that cross section. Stimulations could only be applied in the direction of the plane oscillations to either side of the plant and were, together with the concentration deviations, treated as scalars. Hence the deviation caused by two short stimulations immediately after each other was proportional to the algebraic sum of the two stimulations. The reaction of the plant was calculated from the time-delayed total concentration deviation. This deviation caused by many stimulations at different times was proportional to a sum of weighted stimulations (Johnsson 1971).

In the present extension of the model stimulations can be applied in all directions around the stem of the plant and are to be treated as vectors. The concentration deviation caused by a short stimulation should still be proportional to the measure and fall in the direction of the stimulation. It is not evident, however, that the resulting deviation caused by two short stimulations is proportional to their vector sum.

Clearly the result is depending on the two auxin distributions and how these are added up. Whatever type of auxin distribution we may use it is desirable that the resulting distribution is of the same type and for the addition it should be consistent with the algebraic scalar addition in the special case above.

We will try the same type of distribution as in Johnsson 1971, Appendix A1. When the plant is stimulated in a certain direction this causes a linear deviation (that is a constant gradient) from the mean auxin concentration across the stem of the plant in the same direction. The deviation is purely transversal, i.e. it is a function of the coordinates in the u-v-plane of the internal coordinate system S3.

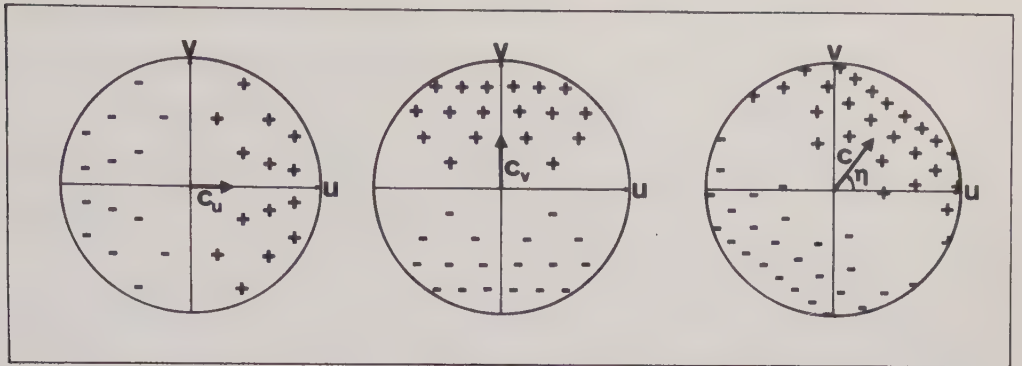


Figure 9. Cross sections of the plant. The cross sections include the u - v -plane of the internal coordinate system S_3 . The $+$ and $-$ signs indicate deviations in the auxin concentration, $+$ meaning excess and $-$ deficit of auxin with respect to the mean concentration. The deviations shown in the left and middle figures are caused by stimulations in the directions of the u - and v -axis respectively. It can be shown that, under certain assumptions, the deviations can be represented by vectors (magnitude c_u and c_v) proportional to the respective stimulation vectors. Consequently the deviation caused by two stimulations (right figure) is represented by their vector sum (magnitude c) as indicated in the figure.

Further, in this paper we assume that the concentration deviations of two auxin distributions, caused by two stimulations immediately after each other, can be added up algebraically in every point of the cross section of the stem.

In order to calculate the resulting auxin distribution it is convenient to express the distributions in polar coordinates (ρ, γ) instead of Cartesian as in Johnsson 1971 (with our notations (u, v)).

Figure 9 shows the two distributions to be summarized (left and middle) and the result (right). The concentration deviations are indicated in the u - v -planes, $+$ meaning excess and $-$ deficit of auxin with respect to the mean concentration.

The first stimulation causes a concentration deviation in the direction of the u-axis (left figure). This deviation can be expressed as $c_U \rho \cos \gamma$, where c_U is a proportionality constant. The deviation caused by the second stimulation is $c_V \rho \cos(\gamma - 90^\circ)$ in the direction of the v-axis (middle figure).

The resulting deviation is

$$\left. \begin{aligned} c_U \rho \cos \gamma + c_V \rho \cos(\gamma - 90^\circ) &= \\ c_U \rho \cos \gamma + c_V \rho \sin \gamma &= \\ c \rho \cos(\gamma - \eta) & \end{aligned} \right\} \quad \begin{aligned} c &= \sqrt{c_U^2 + c_V^2} \\ \tan \eta &= \frac{c_V}{c_U} \end{aligned}$$

In this orthogonal case the resulting deviation (right figure) is of the same type (linear) as the original deviations and it is calculated by vector addition. We realize, without calculation, that this is also valid for parallel deviations. Consequently, any deviation can be decomposed into u- and v-components which means that any two deviations (not necessarily at right angles or parallel) can be summarized by vector addition. Also in this general case the resulting deviation is of the same type (linear). Further, in the special case of parallel deviations, vector addition is equivalent to algebraic scalar addition. Our requirements above about the auxin distributions and their addition are fulfilled.

We have shown that the linear deviations can be treated as vectors. Because of the transverse auxin distribution such a vector is situated in the u-v-plane at right angles to the plant as indicated in Figure 9.

Also the stimulation vector is orthogonal to the plant, more precisely it is claimed that this vector is proportional to the component of gravity at right angles to the plant (Israelsson and Johnsson 1967). Considering the introducing arguments of this section it is now natural to require the deviation vector be proportional to the corresponding stimulation vector. Hence the coordinates (x_1, y_1, z_1) in S2 of the stimulation vector are of interest and analysing the condition above in Israelsson and Johnsson 1967 we get

- (1) The vector is lying in the plane defined by the plumb-line (z-axis) and the plant ($\vec{r}$).
- (2) It is orthogonal to the plant ($\vec{r}$).
- (3) With the same proportionality constant as in previous works the magnitude (length) of the vector is $\sin\alpha$.

Expressed as equations ($\vec{r} = (x, y, z)$).

- (1) $-yx_1 + xy_1 = 0$
- (2) $xx_1 + yy_1 + zz_1 = 0$
- (3) $x_1^2 + y_1^2 + z_1^2 = \sin^2\alpha = x^2 + y^2$

These equations for the coordinates of the stimulation vector have got two solutions. We choose $(xz, yz, -(x^2+y^2))$, which is directed downwards. Below we will refer to the calculation of these coordinates from (x, y, z) as the orthogonality transformation. The coordinates of the stimulation vector in system S3 are obtained by multiplying the coordinate vector by M^{-1} . The result is $(x, y, 0)$ where the w-coordinate is zero as expected.

The coordinates in the u-v-plane of the time-delayed total stimulation vector at the time t , $s_u(t-t_0)$ and $s_v(t-t_0)$, are calculated as sums of weighted u- and v-coordinates in exactly the same way as described for the single sum of weighted stimulations in Mathematical Appendix, Andersen and Johnsson 1972a. For simplicity of notation we shall use the symbolic argument $t-t_0$ when we are in reality referring to this rather complicated weighting procedure. Polar coordinates in the u-v-plane, magnitude $s(t-t_0)$ and direction with respect to the u-axis $\theta(t-t_0)$, of the time-delayed total stimulation vector are then calculated from $s_u(t-t_0)$ and $s_v(t-t_0)$.

Since we are considering plants of constant length $r = 1$, $d\vec{r}$ is orthogonal to $\vec{r}$ and consequently $\left|\frac{d\vec{r}}{r}\right| = |d\vec{r}|$ equal to the angle passed through by the plant during the time dt .

We recall that the reaction of the plant was calculated from the time-delayed total auxin concentration deviation. Every deviation vector is proportional to the corresponding stimulation vector. Hence the magnitude of the time-delayed total deviation vector is proportional to the magnitude $s(t-t_0)$ of the time-delayed total stimulation vector, and with the same constants as in Andersen and Johnsson 1972a

$$\left| \frac{d\bar{r}}{dt}(t) \right| = A \cdot \ln(1 + B \cdot s(t-t_0)).$$

Since $d\bar{r}$ is orthogonal to $\bar{r}$, the vector $\frac{d\bar{r}}{dt}(t)$ is situated in the u-v-plane and for symmetrical plants it is directed contrary to the stimulation vector, i.e. in the direction $\theta(t-t_0) + 180^\circ$ in the u-v-plane. We have got the possibility of including asymmetrical reactions in either direction by adding a positive or negative angle of asymmetry κ .

We are now able to calculate the coordinates of $\frac{d\bar{r}}{dt}(t)$ in system S3.

$$\frac{du}{dt}(t) = \left| \frac{d\bar{r}}{dt}(t) \right| \cos(\theta(t-t_0) + 180^\circ + \kappa) = - \left| \frac{d\bar{r}}{dt}(t) \right| \cos(\theta(t-t_0) + \kappa)$$

$$\frac{dv}{dt}(t) = \left| \frac{d\bar{r}}{dt}(t) \right| \sin(\theta(t-t_0) + 180^\circ + \kappa) = - \left| \frac{d\bar{r}}{dt}(t) \right| \sin(\theta(t-t_0) + \kappa)$$

$$\frac{dw}{dt}(t) = 0$$

We refer to these equations as the set of equations in system S3. This designation is improper inasmuch as the coordinate system S3 is fixed in the plant and moves along with it so that the coordinates of the plant in S3 are always (0, 0, 1). The equations may be interpreted as the change of the coordinates in S3 of the plant if the system S3 was momentarily fixed in the observer's system S2. Further the right members of the equations are calculated using coordinates from S2. In the next section, however, we are going to transform our equations to the observer's system S2. Then it is necessary that all quantities are expressed in coordinates from S2 and then the equations will also deserve their designation. The designation of this section was chosen in order to facilitate the understanding of our main line of reasoning.

3. Set of equations in system S2.

The coordinates in S2 of $\frac{d\bar{r}}{dt}(t)$ are obtained when multiplying the coordinate vector in S3 by the matrix M.

$$\begin{aligned}\frac{dx}{dt}(t) &= - \left| \frac{d\bar{r}}{dt}(t) \right| \cdot \left(\cos(\theta(t-t_0) + \kappa) (\sin^2\phi(t) + \cos\alpha(t)\cos^2\phi(t)) \right. \\ &\quad \left. + \sin(\theta(t-t_0) + \kappa) \cos\phi(t)\sin\phi(t)(\cos\alpha(t) - 1) \right) \\ &= - \left| \frac{d\bar{r}}{dt}(t) \right| \cdot \left(\cos\alpha(t)\cos\phi(t)\cos\psi(t) + \sin\phi(t)\sin\psi(t) \right)\end{aligned}$$

$$\begin{aligned}\frac{dy}{dt}(t) &= - \left| \frac{d\bar{r}}{dt}(t) \right| \cdot \left(\cos(\theta(t-t_0) + \kappa) \cos\phi(t)\sin\phi(t)(\cos\alpha(t) - 1) \right. \\ &\quad \left. + \sin(\theta(t-t_0) + \kappa) (\cos^2\phi(t) + \cos\alpha(t)\sin^2\phi(t)) \right) \\ &= - \left| \frac{d\bar{r}}{dt}(t) \right| \cdot \left(\cos\alpha(t)\sin\phi(t)\cos\psi(t) - \cos\phi(t)\sin\psi(t) \right)\end{aligned}$$

$$\begin{aligned}\frac{dz}{dt}(t) &= - \left| \frac{d\bar{r}}{dt}(t) \right| \cdot \left(\cos(\theta(t-t_0) + \kappa) (-\sin\alpha(t)\cos\phi(t)) \right. \\ &\quad \left. + \sin(\theta(t-t_0) + \kappa) (-\sin\alpha(t)\sin\phi(t)) \right) \\ &= \left| \frac{d\bar{r}}{dt}(t) \right| \cdot \left(\sin\alpha(t)\cos\psi(t) \right)\end{aligned}$$

where $\psi(t) = \phi(t) - \theta(t-t_0) - \kappa$.

Omitting the argument t we have

$$(Re) \quad \left\{ \begin{array}{l} \frac{dx}{dt} = \left| \frac{d\bar{r}}{dt} \right| \cdot (-\cos\alpha \cos\phi \cos\psi - \sin\phi \sin\psi) \\ \frac{dy}{dt} = \left| \frac{d\bar{r}}{dt} \right| \cdot (-\cos\alpha \sin\phi \cos\psi + \cos\phi \sin\psi) \\ \frac{dz}{dt} = \left| \frac{d\bar{r}}{dt} \right| \sin\alpha \cos\psi \end{array} \right.$$

Differentiating the relations

$$\left\{ \begin{array}{l} x = r \sin\alpha \cos\phi \\ y = r \sin\alpha \sin\phi \\ z = r \cos\alpha \end{array} \right.$$

with $r = 1$, and inserting into (Re) we find

$$(Sp) \quad \left\{ \begin{array}{l} \frac{d\alpha}{dt} = \left| \frac{d\bar{r}}{dt} \right| \cdot (-\cos\psi) \\ \frac{d\phi}{dt} = \left| \frac{d\bar{r}}{dt} \right| \frac{\sin\psi}{\sin\alpha} \\ \left(\frac{dr}{dt} = 0 \right) \end{array} \right.$$

In the next section we shall discuss the solution of these equations.

4. Methods of solution.

At first sight the set of equations (Sp = spherical coordinates) seems simpler than (Re = rectangular coordinates). (Sp) is solved only for the two independent variables α and ϕ (r is constant) and the right members seem to be easier to calculate than in (Re).

However, (Sp) includes $\left| \frac{d\bar{r}}{dt} \right|$, which is a function of $c(t-t_0)$, and ψ , which is a function of $\theta(t-t_0)$. $c(t-t_0)$ and $\theta(t-t_0)$ are calculated from a sum of stimulation vectors and when summarizing these vectors we need their rectangular coordinates. They are obtained from the rectangular coordinates of $\bar{r}$, which can of course be calculated from α and ϕ , but the seeming simplicity of (Sp) is then gone. Moreover the angle ϕ has got a discontinuity of 180° when $\bar{r}$ passes the position $(0, 0, 1)$ in S^2 ($\frac{d\phi}{dt}$ infinite) and also in the vicinity of that position ϕ varies very swiftly. This is a serious disadvantage as our equations have to be solved numerically.

From (Re) it is immediately clear that besides solving the equations for the rectangular coordinates, we have to calculate spherical coordinates from these rectangular coordinates. This causes a good deal of computation labour, but it is not so hard to accept since, after all, we use both types of coordinates when presenting the results.

The solution of (Re) produces 3 coordinates i.e. redundant information. The z-coordinate is not necessary for the presentation of the results, but may be used to check the relation

$$\sqrt{x^2 + y^2 + z^2} = r = 1.$$

Estimating that (Sp) and (Re) would require approximately the same amount of computation labour, we have preferred (Re) to (Sp) mainly to avoid the mentioned discontinuity of the angle ϕ .

Most of Mathematical Appendix, Andersen and Johnsson 1972a is applied when solving (Re). The weighting procedure for the sum of stimulation vectors has already been mentioned in section 2 and the iteration method for the solution of the differential equations will be considered below.

In the Appendix there are, however, some improprieties that must first be corrected.

The starting equation of the Appendix

$$\frac{d\alpha}{dt}(t) = - A \cdot \ln\left(1 + B \cdot \int_1^{\infty} f(n) \sin \alpha(t - nt_0) dn\right) \quad (1)$$

was derived by Johnsson 1971 considering only the reaction to one short stimulation with positive α giving a positive integral value. Further it was assumed that $f(n) = e^{-\beta(n-1)}$, $n \geq 1$.

In Andersen and Johnsson 1972 we have used a more realistic weighting function $f(n)$, depicted in Figure A1 of the Appendix. With this function the integration should range from zero to infinity and the integral in equation (1) changes to

$$I(t) = \int_0^{\infty} f(n) \sin \alpha(t - nt_0) dn.$$

Neither α nor $I(t)$ are always positive. Since the reaction has to be of the same magnitude whether $I(t)$ is positive or negative, we actually used the slightly modified equation

$$\frac{d\alpha}{dt}(t) = - \text{sign}(I(t)) \cdot A \cdot \ln(1 + B \cdot |I(t)|). \quad (1')$$

The weighting function in Figure A1 contains a minor intricate fault. The time t_0 shown in the figure is actually 29 minutes instead of 30 minutes as stated in the Figure legend. As mentioned in Andersen and Johnsson 1972a, the geotropic reaction time t_0 in the experiments was chosen as the time from the start of a geotropic pulse until the plant had bent $0.5^\circ - 1.0^\circ$ from its initial position. When the weighting function was adapted to suit this condition, it turned out that t_0 in Figure A1 had to be 29 minutes in order to make the geotropic reaction time t_0 equal to 30 minutes. This is so because the theoretically calculated reaction must be allowed to grow from zero for a certain time before it reaches the experimentally detectable magnitude of $0.5^\circ - 1.0^\circ$.

Hence the internal t_0 of the weighting function in Figure A1 is always slightly shorter than the externally measured geotropic reaction time t_0 . This also applies when, as in all our calculations, t_0 varies with the stimulation angle. We regret that this difference has not been mentioned in previous papers.

The formulas for $I(t)$ and $I(t+1)$ in the Appendix are most easily corrected by changing $I(t)$ for $I(t-1)$ and $I(t+1)$ for $I(t)$.

In the trapezium formula for the approximation of an integral, n should be changed for m since n is already used in the integral in equation (1) of the Appendix. n is an unsuitable integration variable, but it is retained from previous works.

Since the trapezium formula is used for calculating the integral, the same method should also, for the sake of consequence, be used for the iteration in the differential equation instead of formula (3) of the Appendix.

Like formula (3) the trapezium method of iteration can be used thanks to the knowledge of derivatives in advance of the function. Formula (3) offers a slightly better convergence, but with our short iteration interval this is not needed. When equation (1') was solved using either formula, the difference between corresponding values of the resulting angle α never exceeded 0.02° during 1500 minutes (10 oscillations), which should be compared to the amplitude 24° .

So far the corrections of Appendix A1.

The set of equations (Re) of this paper was solved with the aid of a digital computer. The same iteration interval, 1 minute, as in the Appendix above was used. Since the derivatives of the present equations are not known in advance of the functions (see section 3) we had to use a slightly inferior variant of the trapezium method of iteration, called Heun's method. A comparison between this method in the special case of plane oscillations and the trapezium method in equation (1') will be given in section 6.

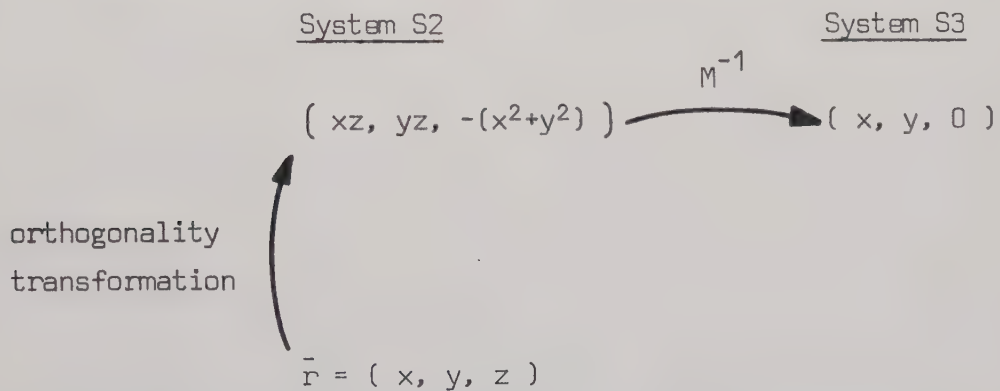
5. The application of gravitational stimulation pulses.

Applying a gravitational pulse to the plant with the stimulation angle A in the direction ϕ means tilting the coordinate system S2 the angle A in the direction ϕ with respect to a coordinate system S1 (X-Y-Z), fixed in space.

The transformation matrix between S2 and S1 is called N . N is easily calculated from M by exchanging α for A and ϕ for Φ .

In section 2 we calculated the coordinates in S3 of the stimulation vector by first applying the orthogonality transformation to the coordinates in S2 of $\bar{r}$ and then transforming the coordinates thus obtained to S3 by multiplying the coordinate vector by M^{-1} .

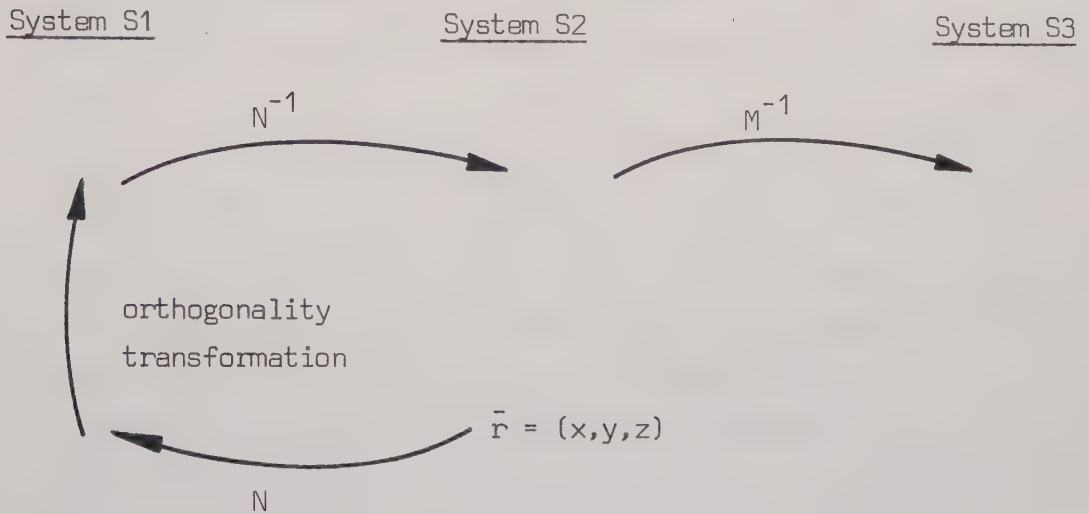
Schematically:



In the present situation system S1 is fixed in space and it is the Z-axis instead of the z-axis that is parallel to the plumb-line.

Hence the orthogonality transformation has to be made in system S1. For that purpose the coordinates in S2 of $\bar{r}$ must first be transformed to S1. The orthogonality transformation is then executed and the coordinates obtained transformed back to S2 and finally to S3.

Schematically:



We estimated that calculating a final result once for all, that is u,v and w-coordinates like in section 2, would be laborious. The w-coordinate would be zero, it is true, but the other coordinates would not by far be as simple as in section 2, where we benefited by $\bar{r}$ and M^{-1} containing the same angles, while in the present case the new angles of tilting are also involved. Since besides, gravitational pulses are rather rare, we have chosen to let the computer carry out all the matrix multiplications, and also to check that the w-coordinate obtained is zero.

6. Theoretical test of the extended model.

Apart from the physiological assumption about auxin distributions and their addition, the extension of the present paper is purely mathematical. We have established that the addition is consistent with the corresponding addition in the previous model for plane oscillations. We have also pointed out that all constants have got the same values as earlier.

In the special case of plane oscillations we therefore expect exactly the same simulation results as earlier, except for approximation errors, introduced by the numerical methods of solution.

To test this the coordinates in S2 of the vector $\bar{r}$, together with the angles α and ϕ , were calculated in the special case of plane oscillations. 6 different runs, with oscillations in 6 different planes through the z-axis, were executed. The plant was started in 6 different directions by pulses of the same magnitude and was then allowed to oscillate freely for 1500 minutes.

The plant continued for the whole run to oscillate in the plane defined by the starting pulse. More precisely this means that the angle ϕ was constant with an accuracy of two decimals, except of course for the jump of 180.00° at the passage of the z-axis.

(α and ϕ were printed out from the computer with two decimals)

With the same accuracy, the corresponding values of α in the 6 runs did not differ. The values of α , obtained from the equation of the previous model (section 4) solved with the same starting pulse as the 6 other runs, never differed from the corresponding values of α in the 6 runs by more than 0.02° .

The value of $\sqrt{x^2+y^2+z^2}$ was checked according to section 4. It differed from 1 by at most 0.0001.

According to section 5, we instructed the computer to report if the w-coordinate of the stimulation vector exceeded 0.01 when a gravitational pulse was applied. During all our runs (more than 100) this never happened.

These results indicate that our extension is mathematically correct and that the approximation errors are tolerable.

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